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The Effects of Large Mammalian Herbivores on Plant and Insect Communities in Kenya

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Abstract

Large mammalian herbivore populations in Kenya are declining in numbers because of habitat degradation, fragmentation, and loss. Hunting practices are also a contributing factor. The loss of large mammalian herbivores can have cascading effects in an ecosystem. Interactions between large mammalian herbivores and plants are well known and widely studied, as well as interactions between flowers and their insect pollinators. However, the indirect effects of large mammalian herbivores on insect pollinators have not been as widely studied. This thesis examines the indirect effects that large mammalian herbivores have on insect pollinators. In order to do this, I conducted research at the Mpala Research Centre in Kenya collecting insect pollinators and recording flower species in different herbivore exclosures spanning a wide aridity gradient. These data show that insect pollinator communities respond directly to flower communities, in addition to any direct effects herbivory and rainfall have on insect communities. These results suggest that large mammalian herbivores and rainfall have a significant effect on insect community composition, both through their direct effect on insect pollinator communities and through their effect on flower communities. These results suggest that the loss of large mammalian herbivore populations could negatively affect all levels of the food chain, including insect pollinators.

Preface

First of all, I would like to thank my wonderful thesis advisors Dan Doak, Dale Miller, and Deane Bowers for all of their knowledge and expertise throughout the project. A very special thank you to Allison Louthan who took me under her wing, introduced me to Kenya, and taught me endless skills in the sciences. I would also like to thank everyone at the Mpala Research Centre, especially my field assistants Patrick and Jon, for making my three-month adventure in Kenya enjoyable and safe. Lastly, I want to thank Cole Pazar, and my family and friends for their never-ending patience, love, and support.

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Chapter 1: Introduction

The Late Quaternary extinctions marked the beginning of increasing mammal extinctions worldwide. There is significant controversy over the cause of the Late Quaternary extinctions, but recent studies have found that they were mostly caused by human settlement and colonization. Since then, large mammal extinctions continue to be human caused. Currently, humans are causing extinctions worldwide at alarming rates via increased human settlement, urbanization, agricultural and livestock expansion, and increased commercial poaching, all of which contribute to habitat degradation, fragmentation, and loss. Habitat degradation, fragmentation, and loss then leads to decline in large mammalian population numbers and eventually, extinction.

The loss of large mammalian herbivores could have cascading effects on the whole ecosystem through possible cascading effects on the plant communities in their habitat. For example, excluding large mammalian herbivores in a savannah ecosystem has resulted in increased abundance of unpalatable plant species. While there is strong empirical evidence that mammalian herbivores strongly affect plant communities in a variety of systems, there are fewer studies that look at other cascading effects. In particular, the indirect relationship between large mammal and insect communities is poorly understood.

For my thesis project, I address the question: how will the loss of large mammal species alter the interactions between plant and insect species? In order to answer this question, I spent a combined three months over two trips collecting data in the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) plots at the Mpala Research Centre in the Laikipia district of Kenya. The UHURU plots are designed to exclude specific size classes of herbivores at different levels of rainfall, mimicking loss of large mammalian herbivores in different climate change scenarios.

Four treatments (three exclude mammalian herbivores of differing sizes, and one is open to all mammalian herbivores) are replicated three times at each of the three sites spanning a strong aridity gradient. At each of these locations, I collected insect species with pan traps and recorded flowering species present in both the dry (January – February) and the wet (May – June) season. These data will show the interactions between flower species and insect species, and will provide insight to the effect that large mammals have on these communities.

Chapter 2: Background

2a. Large Mammalian Herbivores in Late Quaternary Extinctions

Causes of the Late Quaternary megafauna extinctions have been debated for many years. Recent evidence suggests these extinctions were largely human-caused, which supports Paul Martin's overkill hypothesis (Martin, 1967): that the Late Quaternary extinctions were caused by excessive human predation (Bartlett et al., 2015; Surovell et al. 2015). A 2005 study done by Bartlett et al. compared the time of human colonization around the world to the time of the extinctions, and concluded that human colonization was most likely the dominant driver of the extinctions, although climatic factors were also important (Bartlett et al., 2015). Human colonization and population expansion lead to increased hunting of megafauna which was most likely the main driver of the Late Quaternary extinctions (Bartlett et al., 2015; Surovell et al., 2015). During the Late Quaternary extinctions, there were 24 large mammal (>5 kg) extinctions in continental Africa (Faith, 2014). These 24 mammals accounted for 14% of Africa's large mammal species and made up 25% of the megafauna (Faith, 2014).

2b. Current Threats to Large Mammalian Herbivores

There is very high mammal diversity along the equator in Africa, which makes it a crucial habitat to protect (Vié et al., 2009). Yet, mammal populations are declining rapidly because of hunting along with habitat loss, degradation, and fragmentation (Vié et al., 2009; Wato et al., 2006). The International Union for Conservation of Nature (IUCN) 2008 assessment estimates 22% (1,219 species) of the world's known mammals are threatened or extinct, with 15% of mammals being data deficient (Vié et al., 2009). The IUCN 2008 assessment recorded 107 mammal extinctions since the year 1500 and discovered that 30% of the mammal

populations that remain today are decreasing in size (Vié et al., 2009). Mammal population decline can be attributed to several factors: habitat loss and degradation through agricultural and livestock expansion (Mose & Western, 2015; Ogutu et al., 2011), increased human settlement and urbanization (Mose & Western, 2015; Ogutu et al., 2011), and increased hunting rates (Fa et al., 2002; Wato et al., 2006; Watson et al., 2013; Wittemyer et al., 2014).

One of the largest drivers of mammal population decline is change in habitat through loss, degradation, and fragmentation (Fa et al., 2002; Mose & Wester, 2015; Ogutu et al., 2011; Wato et al., 2006; Watson et al., 2013; Wittemyer et al., 2014). In Kenya, agricultural and livestock expansion is having devastating effects on wild ecosystems because it degrades the natural habitat, over-crowds the land, and fragments natural habitats (Mose & Western, 2015; Ogutu et al., 2011). A long-term study done on wildlife populations in the Mara region of Kenya from 1977 to 2009 shows that wildlife populations are decreasing because of increased livestock populations (Ogutu et al., 2011). Livestock numbers now exceed all wildlife numbers in the Mara region, with the exception of buffalo (Ogutu et al., 2011). Livestock production is causing over-crowding for wild species and is degrading the quality of the land as a result of grazing practices (Mose & Western, 2015; Ogutu et al., 2011).

Agricultural expansion is also causing over-crowding in Kenya and is pushing out the wild species. A long-term spatial cluster analysis in Amboseli National Park, Kenya shows that from 1970 to 2010 elephant and buffalo populations showed the largest reduction of any other mammals in their range due to the fact that they are the most vulnerable to human displacement and land degradation (Mose & Western, 2015). Large mammals like these require a large habitat to survive, and without it will become overcrowded and forced into lower-quality habitat.

Another important driver of mammal population decline is hunting practices. Traditionally, hunting practices have been for individual subsistence purposes of native peoples, but recent studies have demonstrated a greater impact of commercial hunting than traditional practices (Wato et al., 2006). These commercial hunting practices are larger in scale than subsistence hunting and can cause overharvesting. Overharvesting wildlife for human consumption lowers species occurrence and density and therefore is the second largest driver of biodiversity loss and local extinctions (Wittemyer et al., 2014). A study by Fa et al. (2002) showed that 60% of mammals in the Congo Basin are exploited because they are being hunted at a faster rate than they can reproduce (Fa et al., 2002). Many of the mammals in the Congo Basin have long gestation periods and large body sizes, meaning the rate at which they are being hunted is unsustainable.

Recently, hunting rates have risen causing further decline of mammalian herbivore populations. For example, illegal elephant killing in the Samburu National Park of Kenya was higher from 2009 to 2012 than every year since the beginning of monitoring in 1998 (Wittemyer et al., 2014). The Samburu elephant population now has strongly skewed sex ratios, social disruption, and increased orphans (Wittemyer et al., 2014). All of these will likely have a negative impact on the elephant populations in Samburu National Park, leading to further population decline.

Another example of the negative impacts of hunting on mammalian herbivores from a study done by Watson et al. (2013) studied spatial patterns of snare poaching in Zambia. Snaring is considered one of the most significant conservation threats in Africa because it reduces the population of both target species and accidentally caught non-target species (Watson et al., 2013; Fa et al., 2002). This study found that snaring is concentrated where there is the most human

development: Game Management Areas (buffer zones) and areas adjacent to National Parks (Watson et al., 2013). This demonstrates a logical relationship between hunting rates and human development. Where there is more human development, there is more hunting. This is most likely because of convenience and proximity of the animals to large human populations (Watson et al., 2013).

The relationships among the different factors causing the decline of large mammalian herbivore populations is very complex. Human development brings about habitat degradation, fragmentation, and loss (Mose & Western, 2015; Ogutu et al., 2011). Hunting rates are also the highest in areas surrounding human development (Watson et al., 2013). Not only does this effect the large mammalian herbivores, but the loss of these populations are felt throughout an entire ecosystem because they negatively affect food webs and ecological processes (Wittemyer et al., 2014). If these losses continue over time, it will cause the decline of all mammalian herbivore populations which will likely also result in significant changes in plant communities.

2c. Effects of Large Mammalian Herbivores on Plant and Flower Species

Large mammalian herbivores have a major effect on plant community composition and structure in their habitats (Augustine & McNaughton, 1996; Cote et al., 2004; Hobbs, 1996; Milchunas & Lauenroth, 1993). Through their grazing patterns, mammalian herbivores can affect plant growth rate, reproduction, survival, nutrient uptake rate, litter quality, energy transfer, soil development, and nutrient and water cycles (Augustine & McNaughton, 1996; Cote et al., 2004). One of the largest factors that determine the extent to which a plant community will be affected by the presence of large mammalian herbivores is the evolutionary grazing history at that site (Hobbs, 1996; Milchunas & Lauenroth, 1993). If a particular site has a long evolutionary history

of grazing, many of the plants will have developed defense mechanisms against the mammalian herbivores (Augustine & McNaughton, 1996; Cote et al., 2004; Hobbs, 1996; Milchunas & Lauenroth, 1993).

Studies have found that different mammals have different impacts on the plant community in their habitat because of their grazing patterns (Augustine & McNaughton, 1996; Cote et al., 2004). One study showed that impala and kudu have highly selective foraging patterns that are affected by the differences in defensive chemical compounds found in particular plant species of in African savannas (Augustine & McNaughton, 1996). This selective foraging allows for slow-growing woody species with particular defensive chemical compounds to thrive, which over time changes the plant community composition (Augustine & McNaughton, 1996). Similarly, elephants in the West African savanna were observed to stress the population of common, palatable shrub species and increase the population of unpalatable shrub species (Augustine & McNaughton, 1996). These studies show that impala, kudu, and elephants all have significant effect on the plant community composition through their grazing habits. Without healthy mammal populations, the plant community composition will change. The extent to which herbivores change the plant community composition are especially pronounced in African savannas, making them an ideal habitat to study these effects (Augustine & McNaughton, 1996).

There are many different mechanisms through which mammalian herbivores affect plant communities. Mammalian herbivores can affect plant community composition directly when they consume the plants and also indirectly by changing the composition and physical structure of plant habitats (Cote et al., 2004). Mammalian herbivores can also change the nitrogen cycles in their habitats by changing the soil and litter quality through their urine and feces which changes the net primary productivity of the plant community (Hobbs, 1996).

All of these different factors demonstrate that mammalian herbivores change plant community composition and can affect multiple trophic levels. Cote et al. found that when grazing White-tailed deer are changing the plant species abundance and diversity, they are also disrupting plant-pollinator relationships because of the change in relative flower abundance and composition (Cote et al., 2004). This means the White-tailed deer has indirect effects on the insect pollinator species that pollinate the plants they eat (Cote et al., 2004). These cascading effects are more likely to be present in ecosystems where many different species of large mammalian herbivores are present (Cote et al., 2004).

2d. Direct Effects of Flower Community Composition on Insect Pollinator Community Composition

Insect pollinators play a key role in the reproduction of many plant species and contribute to healthy ecosystem diversity and function (Ebeling et al., 2008; Potts et al., 2003). Many studies have shown that insect pollinator diversity is strongly related to plant and flower diversity (Ebeling et al., 2008; Potts et al., 2003). The number of flowering plant species and amount of blossom cover are directly correlated to the frequency, diversity, and stability of pollinator visits (Ebeling et al., 2008). In turn, pollinator visits are crucial to the reproductive success and sustained health of the plant communities (Ebeling et al., 2008). These complex plant-pollinator relationships may be essential for the persistence and functioning of entire ecosystems (Klein et al., 2007).

A 2007 study done by Klein et al. found that 80 of the worlds 100 most important staple crops for human use as defined by Prescott-Allen and Prescott-Allen are pollinated by wild insects (Klein et al., 2007; Prescott-Allen & Prescott-Allen, 1990). This means a loss or change

in wild pollinator communities can have devastating effects on crops worldwide. A loss in pollinator diversity could mean plant population decline and extinctions, and therefore a change in plant community composition (Fontaine et al., 2006). In turn, this could change the production of agroecosystems that rely on insect pollinators (Fontaine et al., 2006). Higher trophic level consumers may also be affected because their diversity and biomass are dependent on primary production (Fontaine et al., 2006).

2e. Indirect Effects of Large Mammalian Herbivores on Insect Pollinator Community Composition

It is established that large mammalian herbivore populations are declining. It logically follows that this is most likely changing plant community composition and flower community composition related thereto. A change in flower community composition can change the insect pollinator community composition. Previous research has investigated the direct effects of large mammal herbivory and rainfall on plant and insect species, but insufficient research has been done on the indirect effects herbivory has on insect community composition through flower community composition. For my thesis, I studied the complex relationships among mammalian herbivores, plant and flower community composition, and insect community composition. My research aims to answer the question: how will the loss of large mammal species alter the interactions between plant communities and insect pollinator communities? In particular, does flower community composition (which is directly affected by herbivory) directly affect insect community composition, implying indirect effects of herbivory on insect communities (Fig. 1)? This will tell us if the loss of large mammal populations will indirectly affect insect community composition, and give us even further reasons to preserve and protect large mammal populations.

I tested two hypotheses about the effects of large mammalian herbivores on plant and pollinator communities:

(1) Insect and flower communities are both directly affected by herbivory and aridity, and any correspondence between their communities is due to direct effects of herbivory and aridity (Fig. 1, red and blue arrows).

(2) Insect communities respond to flower communities directly (Fig. 1, green arrow), implying indirect effects of herbivory on insect communities, in addition to any direct effects herbivory and site (aridity) have on insect communities.

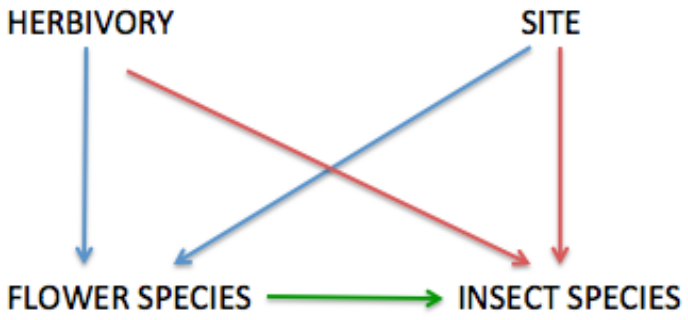

Figure 1. The two hypotheses being tested for the correspondence of insect and flower communities. (1) Insect and flower communities are both directly affected by mammalian herbivory and site, and any correspondence between their communities is due to direct effects of mammalian herbivory and site, as indicated by the red and blue arrows. (2) Insect communities also respond to flower communities directly, as indicated by the green arrow, in addition to any direct effects of mammalian herbivory and site on insect communities as indicated by the red arrows.

Chapter 3: Methods

3a. Field and Lab Methods

The Mpala Research Centre in the Laikipia District of Kenya is located in an arid acacia-dominated savanna. This ecosystem contains a wide range of large mammalian herbivores, the most common of which are: elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and dik-dik (*Madoqua guentheri*) (Louthan et al., 2013).

Research for this project was conducted in the UHURU experiment: large-scale, long-term herbivore exclosures. There are four different herbivore treatment plots in 1-ha plots in a randomized block design using electric fences:

(1) LMH - All Large Mammalian Herbivores (>5 kg) are excluded in the LMH herbivory
(2) MESO - mega- and mesoherbivores (>40 kg) are excluded in the MESO herbivory
(3) MEGA- megaherbivores (elephants and giraffes) are excluded from the MEGA herbivory
(4) Control – Allows access to all mammalian herbivores in Control herbivory

Each herbivore treatment is replicated in 3 different blocks at 3 different sites (making for 9 different blocks): the Arid Site in the North, the Intermediate Site in the middle, and the Mesic Site in the South across a 22-km rainfall gradient (Fig. 2).

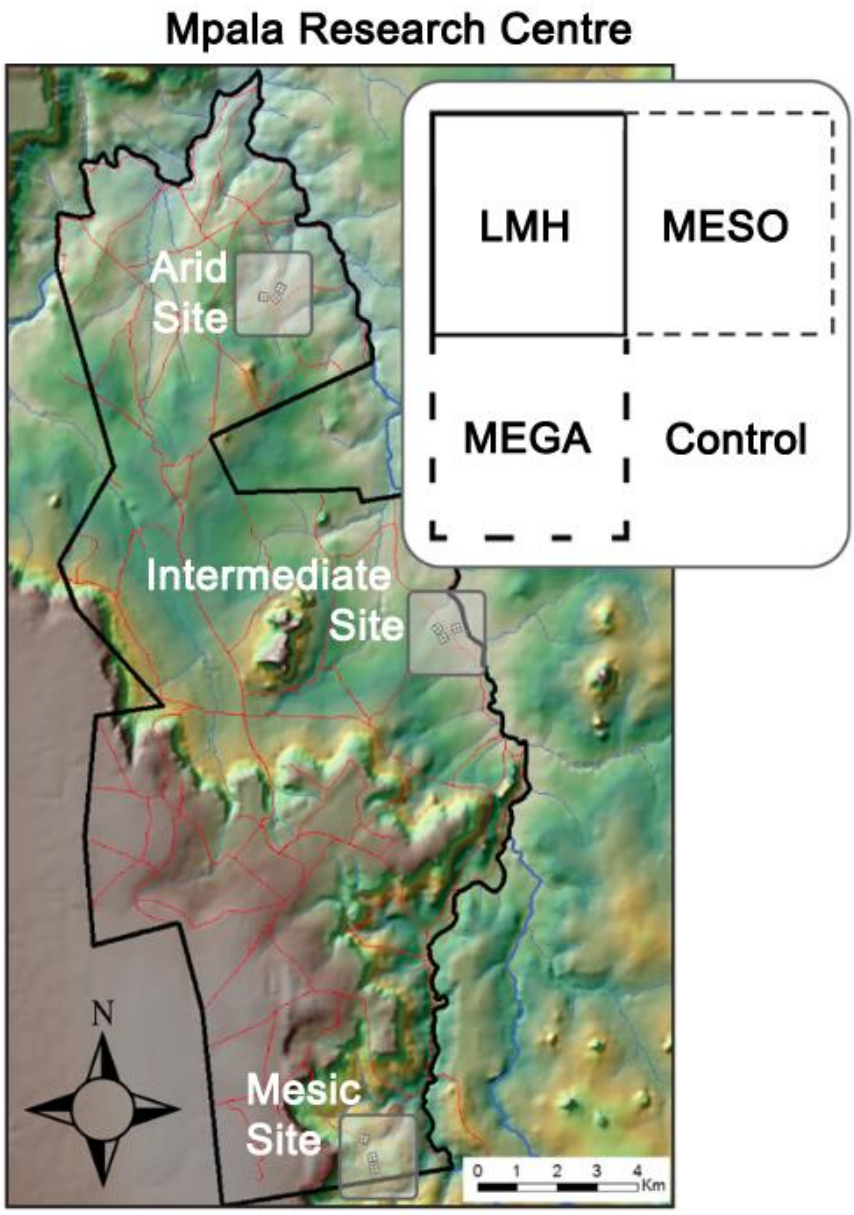

Figure 2. Schematic of the UHURU experiment at the Mpala Research Centre (Adapted from Goheen et al., 2013). The property boundary is outlined in black, and dirt roads are outlined in red. The 3 study sites are shown in grey. Each site contains 3 different blocks, each containing 4 1-ha herbivore exclosure plots, each with 4 different treatments (depicted in the inset).

I sampled all of the nine UHURU plots in both the wet and dry seasons, each with 4 different herbivory treatments in each season. In the wet season, I collected insects in all four herbivory treatments. In the dry season I collected insects in only LMH and Control herbivory treatments because I expected insect density to be lower in the dry season, and was time limited.

To collect insect pollinators, I followed the methods from *Tips on How to Use Bee Bowls to Collect Bees* (Deroge, 2008). I made the pan traps using 3.25 ounce white soufflé cups painted Silical Flat, Yellow Fluorescent, and Blue Fluorescent from East Coast Guerra Paint and Pigment according to the protocol in Deroge's article (Deroge, 2008).

On the first day in a herbivory*block*site*season combination, bowls of each of the 3 colors were placed in trios on the ground, with each trio placed 5 meters apart across the inner 70x70 meter grid of the plot in a cross design for a total of 27 trap locations and a total of 81 cups in each herbivory*block*site*season combination (Fig. 3) To account for an uneven grassy patch or a tree in the way of placing a cup, a 1 meter buffer was allowed along the transect. Cups were laid out in the same order within each herbivory*block*site*season combination, according to rebar placed 10 meters apart. Each of these cups were filled with soapy water in order to lower the surface tension (allowing for smaller insects to sink if they land on the surface) and left in place for 24 hours. The traps for each herbivory*block*site*season combination were placed during a 30 minute window between 8:30 am and 11 am, and were collected 24 hours later (See Appendix 1 & 2 for details). Also on the first day, flower species were recorded within 3 meters of every pan trap. The number of flowers of each specie were quantified using bins of <10, 10 to 50, 50 to 100, and >100 to determine the number of individual flowers per specie within 3 meters of each pan trap.

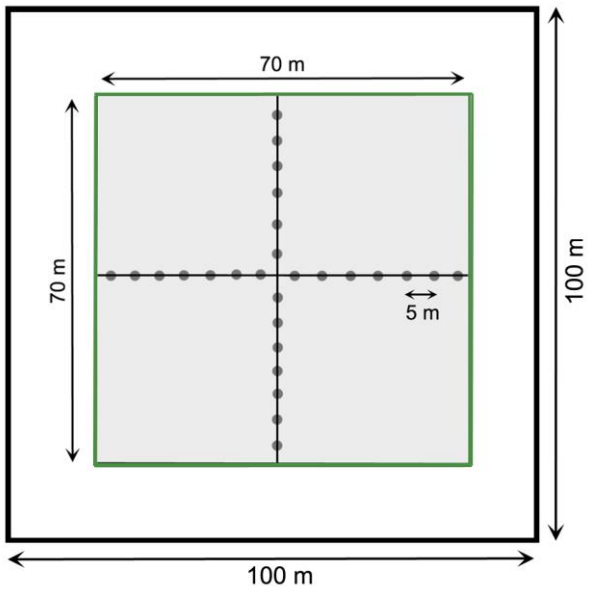

Figure 3. One herbivory*block*site combination found in each UHURU plot. Study site of each plot is the inner 70 meters, indicated by the green square. Pan traps were placed at each grey dot, 5 meters apart from each other.

On the second day, 24 hours later, contents of the pan traps were collected. Contents were kept separated so the exact pan trap location of each insect captured is known. In the lab, insects were first frozen to ensure they were dead, then washed to remove soap residue, and left to dry. Ants, termites, spiders, and grasshoppers were excluded because they are not considered common pollinators in East Africa (Martins, 2014). Insects were then identified to genus or specie with the help of Dino Martins, an East African entomologist. After identification, insects were preserved in 70% ethanol and parafilmed according to protocol in *Tips on How to Use Bee Bowls to Collect Bees* and sent to The National Museums of Kenya in Nairobi, Kenya for storage and display (Deroge, 2008).

3b. Data Analysis Methods

For data analysis, I summed all insect and floral counts for all 27 cup locations in each herbivory*block*site*season combination to determine the species composition. Data from the

dry season (January – February) for Arid Site 3 (which was missing flower community data) and Mesic Site 1 Control (which had no flowers present) were excluded because all of the tests used required a value greater than 0 individuals in the community in order to run the analysis. All densities were log transformed.

I used a three-way Analysis of Variance (ANOVA) to assess the effects of herbivory, site, and season on flower densities and on insect densities. An ANOVA compares these three factors (herbivory, site, and season) testing for variance among them to determine if they are statistically similar.

I used a Detrended Correspondence Analysis (DCA) to find what factors (site, herbivory, or season) influenced flower or insect communities. A DCA identifies the main axes that explain the majority of the variability in the flower or insect community data. A Multivariate Analysis of Variance (MANOVA) tested for combined effects of site, herbivory, and season on the first 2 DCA axes, for both flower and insect communities. I then used an ANOVA to determine if there were singular, separate effects of site, herbivory, and season on these DCA axes. If there were significant ANOVA results, I used a Tukey's HSD post-hoc test to determine which levels of each factors differ from each other. I then plotted the MANOVA residuals of the flower community against the MANOVA residuals of insect community to determine whether insect community tracked flower community, while removing direct effects of site, herbivory, and season. A significant relationship between the residuals of the MANOVA for the effect of site, herbivory, and season on flower community and the residuals of the MANOVA for the effect of site, herbivory, and season on insect community would suggest that insect communities respond directly to flower communities (Fig. 1).

To test for a relationship between flower community composition and insect composition, I regressed insect DCA axis 1 on flower DCA axis 1. To look for similarities in community composition, I conducted a Mantel test on the dissimilarity matrices of these communities. Finally, I conducted a cluster analysis on the actual flower and insect communities, calculated the Robinson-Foulds distance between the flower clusters and the insect clusters, and then used a randomization approach to determine whether the observed Robinson-Foulds distance between clustered insect communities and clustered flower communities was significantly different than expected by chance.

Chapter 4. Results

I observed 97 flower species and analyzed effects of herbivory, season, and site on total flower density with a three way ANOVA. Flower density is defined as the number of flowers found within each site*herbivory*season combination within the 3 meter radius of each pan trap. The ANOVA revealed significant effects of herbivory on flower density, with no significant effect of site or season (Table 1). The LMH and MESO flower densities were greater than the Control flower densities ($p= 0.011$, $p= 0.042$, respectively, Tukey's HSD). This means that the flower densities were greater in the plots that had only smaller herbivores present, and there were lower flower densities in Control where all large mammalian herbivores were present (Fig. 4).

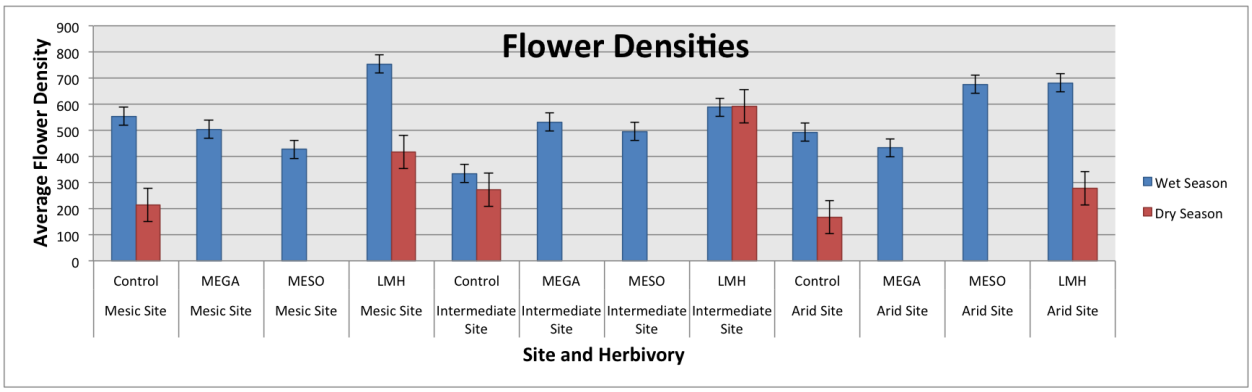

Figure 4. The average flower densities found in each site*herbivory combination. Dry season densities were only recorded in LMH and Control treatments. Error bars are shown as standard error.

Flower ANOVA	F-value	p-value
Site	2.225	0.125
Herbivory	4.559	0.009
Season	2.112	0.156

Table 1. Results of the three-way ANOVA on total flower density.

I collected 84 insect species and analyzed effects of herbivory, season, and site on insect density with a three way ANOVA. Insect density is defined as the number of insects found within each site*herbivory*season combination (81 cups) (total insect densities can be seen in Appendix 3). The ANOVA revealed significant effects of site, with no significant effect of season, nor herbivory on density (Table 2). Mesic Site insect densities were greater than Arid Site insect densities (p= 0.003, Tukey's HSD) (Fig. 5). The relationship between total flower density and total insect density is not significant (p= 0.479) (Fig. 6).

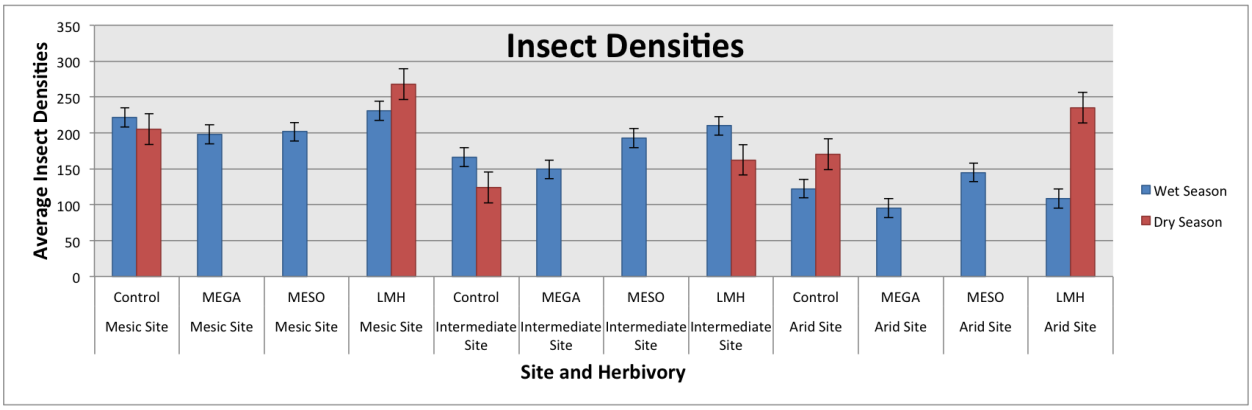

Figure 5. The average insect densities found in each site*herbivory combination. Dry season densities were only recorded in LMH and Control treatments. Error bars are shown as standard error.

Insect ANOVA	F-value	p-value
Site	6.419	0.004
Herbivory	1.434	0.25
Season	1.075	0.307

Table 2. Results of the three-way ANOVA on total insect density.

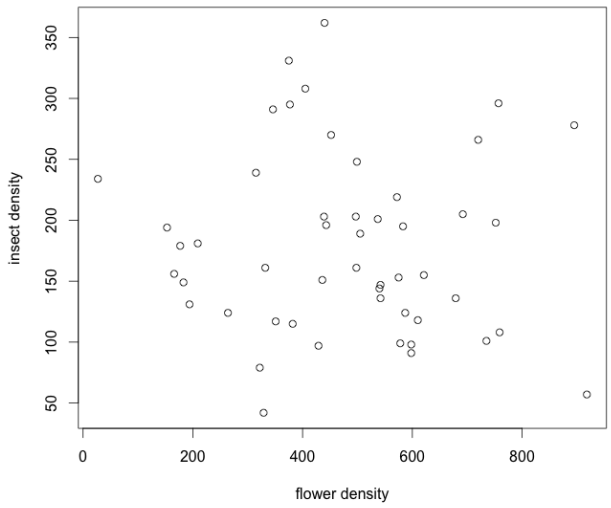

Figure 6. Comparison of flower density and insect density in UHURU plots.

I generated rank abundance curves to examine patterns in relative species abundance. The abundance curves in figure 7 show a ranking of most to least abundant species in that particular site and herbivory treatment on the x-axis and the fraction of total individuals within a specie as a log value. These graphs show the differences between herbivory in each site (Fig. 7). MEGA and Control had high frequency of common flowers in Arid Site and Intermediate Site, while MESO and Control had high frequency of common flowers in Mesic Site. Insect densities were relatively similar, with the exception of LMH Intermediate Site having lower frequency of the common insect densities.

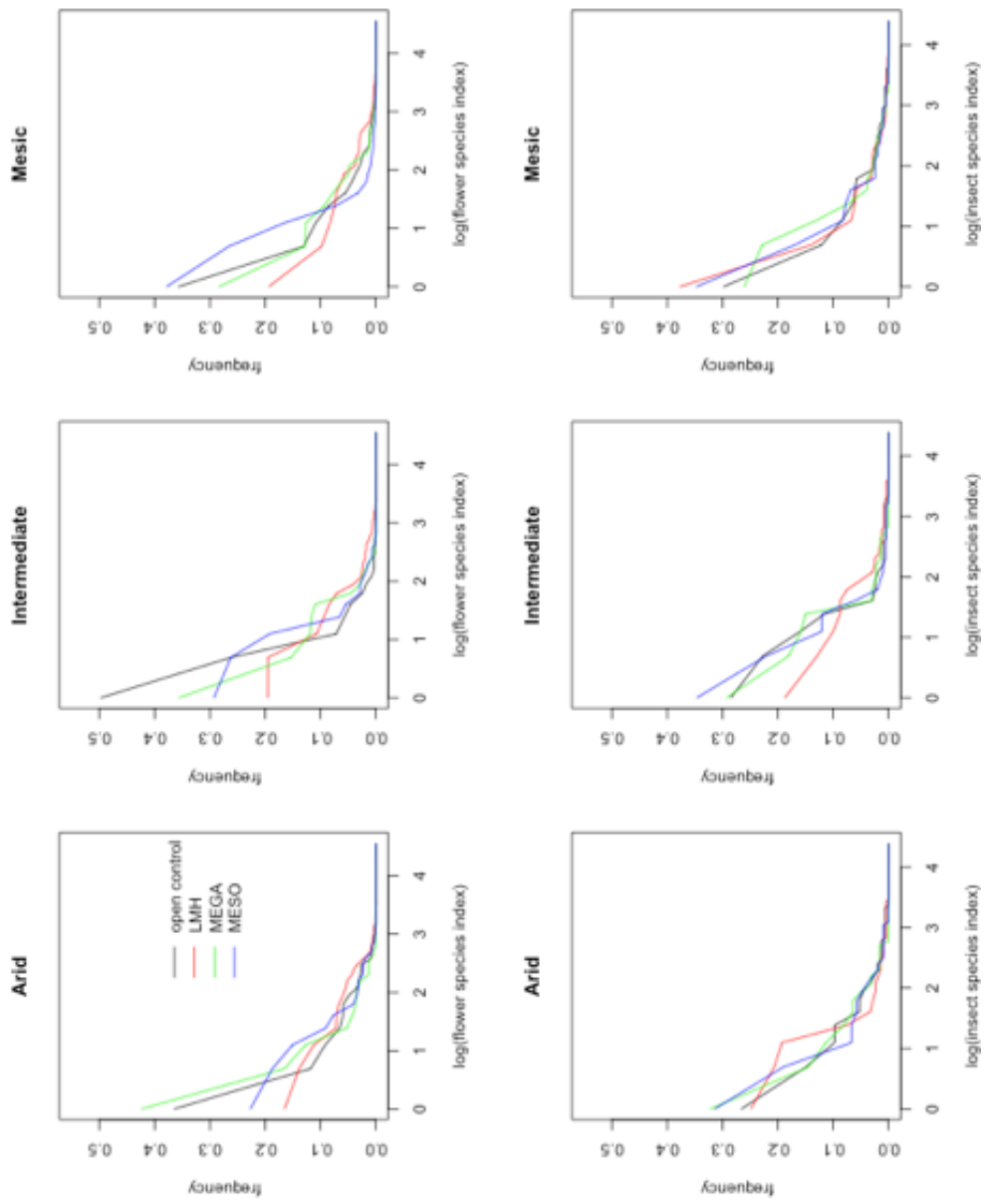

Figure 7. Abundance curves for each different site*herbivory combination shown as the fraction of total number of individuals in log values. The flower or insect species on the x-axis are arranged where 0 is the most common specie found in that site*herbivory combination and 5 is the least common. The y-axis is the fraction of total frequency with which they were found in a given site*herbivory combination, summed over dry and wet seasons

I conducted a DCA on flower community composition. The DCA on flower community revealed that the first 2 axes explain the majority of the variability in flower communities (eigenvalues: 0.83, 0.69, 0.33, 0.28). Site, herbivory, and season have significant effects on the first 2 DCA axes of the flower community (MANOVA, $p<0.05$) (Fig. 8). Across sites and treatments, the flower communities were considerably more similar in the dry season than the wet season as seen in figure 8. Flowers that load the DCA 1 axis positively with a DCA score >2.0 are *Notonia petraea, Kalanchoe lanceolata, Plectranthus cylindraceus, Kleinia squarossa, Acacia etibaica, Baleria spinisepla, Crassula volkensii, Kalanchoe pritwizii, Ipomoea kituensis, Sarcostemma viminale, Acacia brevispica, Justicia odora, Acacia drepanolobium, Plectranthus prostatus, Aerva lanata, Kleinia squarossa, Phyllanthus maderaspatensis, Maerua angolensis,* and *Euphorbia.* Flowers that load the DCA 1 axis negatively with a DCA 1 score <-2.0 are *Ipomoea sinensis, Trubulus terrestis, Osteospermum vaillantii, Pentanisia ouranogye, Phyllostria, Lily, Gutenbergia cordifolia, Cyperus,* and *Oxygonum sinuatum.* The flower specie that loads the DCA 2 axis positively with a DCA score >2.0 is *Euphorbia.* Flowers that load the DCA 2 axis negatively with a DCA score <-2.0 are *Justicia odora, Plectranthus prostatus, Aerva lanata, Kleinia squarossa, Phyllanthus maderaspatensis, Acacia drepanolobium, Acacia brevispica, Baleria spinisepla, Acacia etibaica, Kalanchoe lanceolata, Kalanchoe pritwizii,* and *Sarcostemma viminale* (See Appendix 4 for details).

An ANOVA revealed that site, herbivory, and season all have significant effects on flower DCA axis 1 (Table 3). A Tukey's HSD revealed that the Intermediate Site DCA 1 scores are higher than the Arid Site's. LMH DCA 1 scores are greater than Control, MEGA, and MESO's DCA 1 scores, and that dry season DCA 1 scores are greater than wet season DCA 1 scores. Only site has a significant effect on flower DCA axis 2 (ANOVA: $F= 5.794$, $p =0.006$),

but season is marginally significant (F= 3.868, p= 0.056). A Tukey's HSD revealed that the Arid Site DCA 2 scores are greater than the Mesic Site, and the wet season are greater than the dry season.

Flower DCA 1 ANOVA	F-value	p-value
Site	3.547	0.038
Herbivory	12.605	5.18E-06
Season	117.971	8.99E-14

Table 3. Results of the ANOVA on flower DCA axis 1.

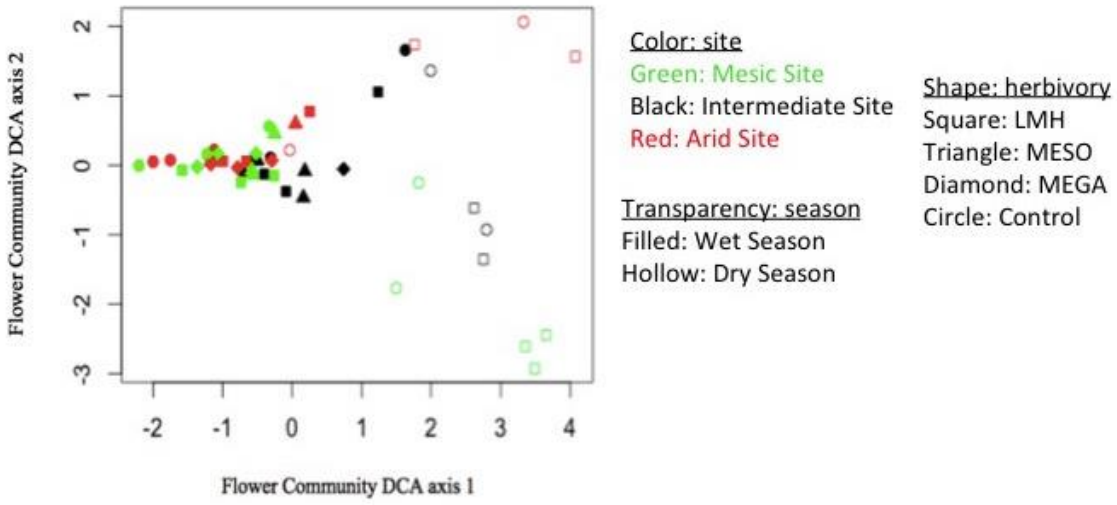

Figure 8. Community composition of flower communities along the first 2 DCA axes. Individual points indicate herbivory*block*site*season combinations. Hollow dots indicate January-February data (dry season). Filled dots indicate May-June data (wet season). Colors indicate aridity level (green: Mesic Site, black: Intermediate Site, red: Arid Site), and shapes indicate treatment (square: LMH, triangle: MESO, diamond: MEGA, circle: Control).

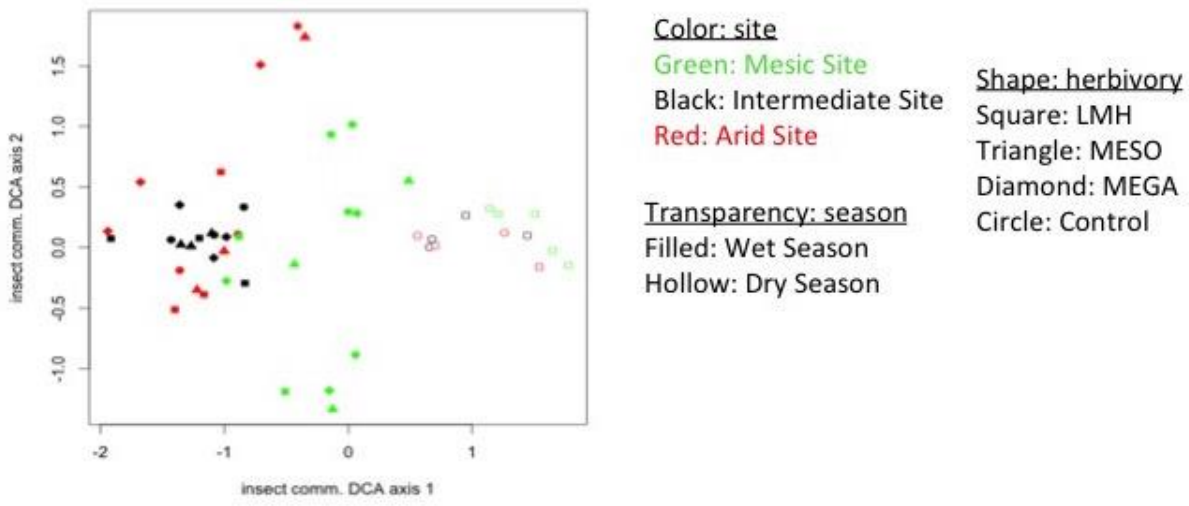

Figure 9. Community composition of insect communities along the first 2 DCA axes. Individual points indicate herbivory*block*site*season combinations. Hollow dots indicate January-February data (dry season). Filled dots indicate May-June data (wet season). Colors indicate aridity level (green: Mesic Site, black: Intermediate Site, red: Arid Site), and shapes indicate treatment (square: LMH, triangle: MESO, diamond: MEGA, circle: Control).

I conducted a parallel DCA on the insect community composition which revealed that the first 2 axes explain the majority of the variability in insect communities (eigenvalues: 0.64, 0.42, 0.26, 0.17). Insects that load the DCA 1 axis negatively with a DCA 1 score <-2.0 are *Scarabaeidae*, *Oruza*, *Chrysodeixes*, and *Cerambycidae*. Insects that load the DCA 1 axis positively with a DCA 1 score >2.0 are *Hypeninae*, Unknown 1, *Colletes*, *Reduvidae*, *Braunsapis*, *Pyralidae*, *Multillidae*, *Battidae*, *Periplaneta*, *Eumenidae*, *Blattodea*, *Plebeina*, *Meliodae*, and *Megachile*. Insects that load the DCA 2 axis negatively with a DCA 2 score <-2.0 are *Sarcophagidae*, *Scoliidae*, and *Masarinae*. Insects that load the DCA 2 axis positively with a DCA 2 score >2.0 are *Cacyreus lingeus*, *Curculionidae*, *Crambidae*, and *Vespoidea* (See Appendix 5 for details).

MANOVA results of insect community DCA axis 1 and DCA axis 2 show that site, herbivory, and season all have significant effects on insect community DCA axis 1 and DCA axis 2 (Fig. 9) (Table 4). The insect communities converged in the dry season and were very variable in the wet season, which is the opposite of the flower communities. An ANOVA revealed that site, herbivory, and season all have significant effects on insect DCA axis 1 (Table 5). A Tukey's HSD showed that the Mesic Site DCA 1 scores are greater than the Intermediate Site and the Arid Site's, Control is greater than MEGA and MESO, LMH is greater than MEGA and MESO, and dry season is greater than wet season. An ANOVA revealed that site, season, and herbivory have no significant effect on insect DCA axis 2.

Insect DCA 1 & 2 MANOVA	**F-value**	**p-value**
Site	10.274	8.05E-07
Herbivory	6.076	2.56E-05
Season	95.111	< 3.977e-16

Table 4. Results of the MANOVA on Insect DCA axis 1 and 2.

Insect DCA 1 ANOVA	**F-value**	**p-value**
Site	27.729	2.10E-08
Herbivory	16.855	2.46E-07
Season	176.736	< 2.2e-16

Table 5. Results of the ANOVA on insect DCA axis 1.

Flower community DCA scores are highly correlated with insect community DCA scores: regression of the first DCA axis of both community types is significant (p= 7.73e-10) with an r^2 of 0.556 (Fig. 10; Table 6).

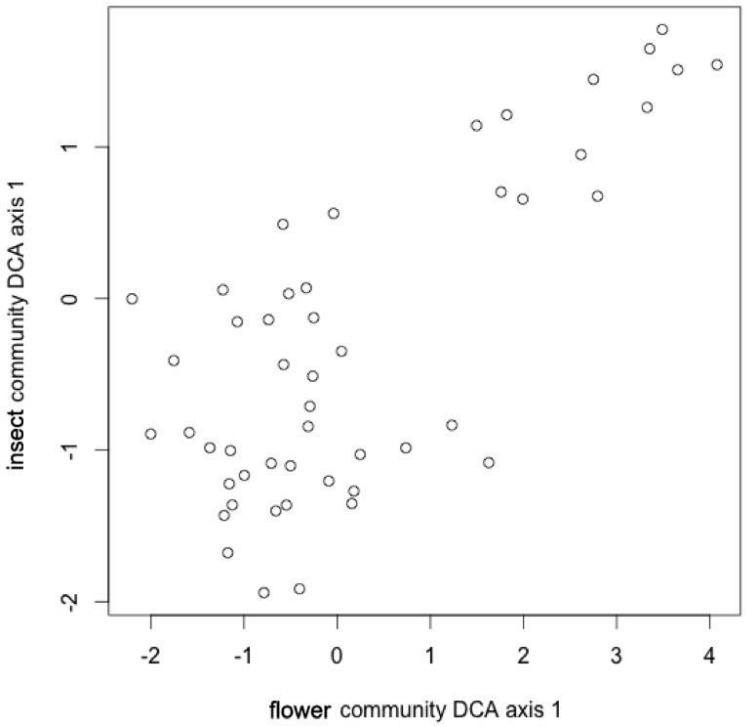

Figure 10. Relationship between flower community DCA 1 and insect community DCA 1.

To test whether insect community tracks flower community while accounting for separate effects of site and herbivory, I ran a MANOVA on the residuals. This showed a significant relationship between the residuals of the MANOVA for the effect of site, herbivory, and season on flower community and the residuals of our MANOVA for the effect of site, herbivory, and season on insect community: The residuals for the first flower DCA axis significantly affect the residuals for the insect DCA axes (MANOVA, $F = 3.867$, $p = 0.028$), but the second flower DCA axis does not ($F= 1.829$, $p= 0.172$) (Fig. 11). An ANOVA indicates that the residuals of the first flower DCA axis significantly affect the residuals of the first insect DCA axis ($F = 7.568$, $p= 0.008$), but the residuals of neither flower axis affect the second insect DCA axis ($p>0.05$).

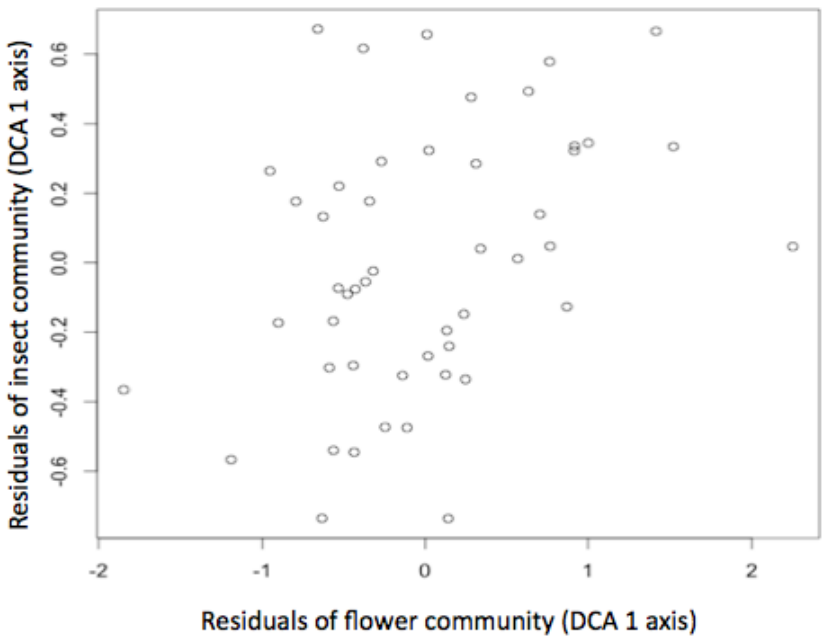

Figure 11. MANOVA residuals from flower community DCA axis 1 and insect community DCA axis 1.

I found a significant correlation between the Bray-Curtis dissimilarity values between pairs of flower communities and insect communities, suggesting a strong relationship between flower and insect community composition (Mantel rho = 0.284, p= 0.001). Finally, I assessed the clustering patterns of flower and insect communities and found the Robinson-Foulds distance between these clustering patterns. I found that this distance was significantly smaller than would arise by chance by randomizing insect community identity (p= 0.05), and thus that the clustering patterns of flower communities were highly correlated with those of insect communities.

	Insect DCA 1	**Insect DCA 2**	**Flower DCA 1**
Insect DCA 1			
Insect DCA 2	0.01995675		
Flower DCA 1	0.7459272	-0.02966	
Flower DCA 2	-0.3052065	-0.00476503- -0.0047	-0.2170941

Table 6. Correlation matrix of the DCA axes.

Chapter 5. Discussion

The results reveal that the presence of large mammalian herbivores affects the flower community composition. If large mammalian herbivore populations continue to decline, this will directly change the plant and flower community composition. There was a significant relationship between the residuals of the flower community MANOVA and the residuals of the insect community MANOVA. Therefore, insect communities respond to flower communities directly, in addition to any direct effects herbivory and site have on insect communities. This suggests that insect community composition is indirectly affected by large mammalian herbivores through changes in flower community composition. I also found that site significantly affects insect communities and that insect density at the Mesic Site was higher than the Arid Site. This is an important connection to recognize as our global climate warms. It is hypothesized by many scientists that the climate in Kenya will become dyer and warmer over time with climate change (Kirtman et al., 2013). This suggests that as climate change continues, insects, including insect pollinators, in the Mesic Site will be forced out of their habitat in search of more mesic habitats where they thrive. A warmer climate could mean the insects that live in the Arid Site will thrive and their habitat will expand, while the ones in the Mesic Site either die off or migrate, changing the entire insect community composition.

Making these observations within the UHURU experiment allowed me to better test for the possible causes of the different patterns I found. The different herbivore treatments and rainfall gradient throughout the Mpala Research Centre gave me a clear understanding of the direct and indirect effects herbivory and rainfall had on flower and insect species. In my experiment I was not able to study which insects are the most effective pollinators, and therefore I was not able to analyze how efficient and effective individual pollinators were to the flower

species in the area. It is important to understand the plant-pollinator interactions to determine how successful a pollinator is to the different plant species in their habitat.

It is imperative that we preserve and protect large mammalian herbivores for the sake of all trophic levels. Not only will the loss of large mammalian herbivore populations affect other mammals and plants, but also the results of my study show that this can also indirectly affect insect communities. Loss or significant change in insect pollinator community composition could have devastating effects for human crops as well as having impacts at other trophic levels. Changes in insect community composition could result in effects on higher trophic level consumers which rely on primary production for their diversity and biomass (Fontaine et al., 2006). This could not only change wild community compositions, but also have severe effects on human crops, many of which heavily rely on wild insect pollinators (Klein et al., 2007).

This research has shown the interconnectivity of wild ecosystems and their wildlife communities and how a change in one trophic level can have cascading effects to other trophic levels. The loss of large mammalian herbivores through hunting along with habitat degradation, fragmentation, and loss can affect plant and insect communities throughout the ecosystem. In order to protect and preserve one trophic level, we must protect and preserve all trophic levels. With threats to large mammalian herbivores increasing, I suggest we start with formulation, implementation, and regulation of habitat management programs and techniques that both preserve large mammalian herbivores and recognize the needs of all trophic levels within the habitat. Adoption and enforcement of strict hunting laws along with community based education about the importance of preserving large mammalian herbivores will also help to preserve these habitats. It is only thorough a comprehensive approach that we can preserve and conserve the wild ecosystems that remain.

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Appendices

Appendix 1. Dates and times pan traps were placed and collected at each site in the dry season.

LOCATION	CUPS PLACED		CUPS COLLECTED	
Intermediate 2 Control	1/23/15	9:30 - 10:00	1/24/15	9:30 - 10:00
Intermediate 2 LMH	1/23/15	10:00 - 10:30	1/24/15	10:00 - 10:30
Mesic 2 LMH	1/26/15	8:30 - 9:00	1/27/15	8:30 - 9:00
Mesic 2 Control	1/26/15	9:00 - 9:30	1/27/15	9:00 - 9:30
Arid 2 LMH	1/28/15	9:30 - 10:00	1/29/15	9:30 - 10:00
Arid 2 Control	1/28/15	10:00 - 10:30	1/29/15	10:00 - 10:30
Intermediate 3 Control	1/30/15	8:30 - 9:00	1/31/15	8:30 - 9:00
Intermediate 3 LMH	1/30/15	9:00 - 9:30	1/31/15	9:00 - 9:30
Mesic 3 LMH	2/2/15	8:15 - 8:45	2/3/15	8:15 - 8:45
Mesic 3 Control	2/2/15	8:45 - 9:15	2/3/15	8:45 - 9:15
Arid 3 Control	2/4/15	9:00 - 9:30	2/5/15	9:00 - 9:30
Arid 3 LMH	2/4/15	9:30 - 10:00	2/5/15	9:30 - 10:00
Arid 1 LMH	2/6/15	9:00 - 9:30	2/7/15	9:00 - 9:30
Arid 1 Control	2/6/15	9:30 - 10:00	2/7/15	9:30 - 10:00
Mesic 1 LMH	2/9/15	9:00 - 9:30	2/10/15	9:00 - 9:30
Mesic 1 Control	2/9/15	9:30 - 10:00	2/10/15	9:30 - 10:00

Appendix 2. Dates and times pan traps were placed and collected at each site in the wet season.

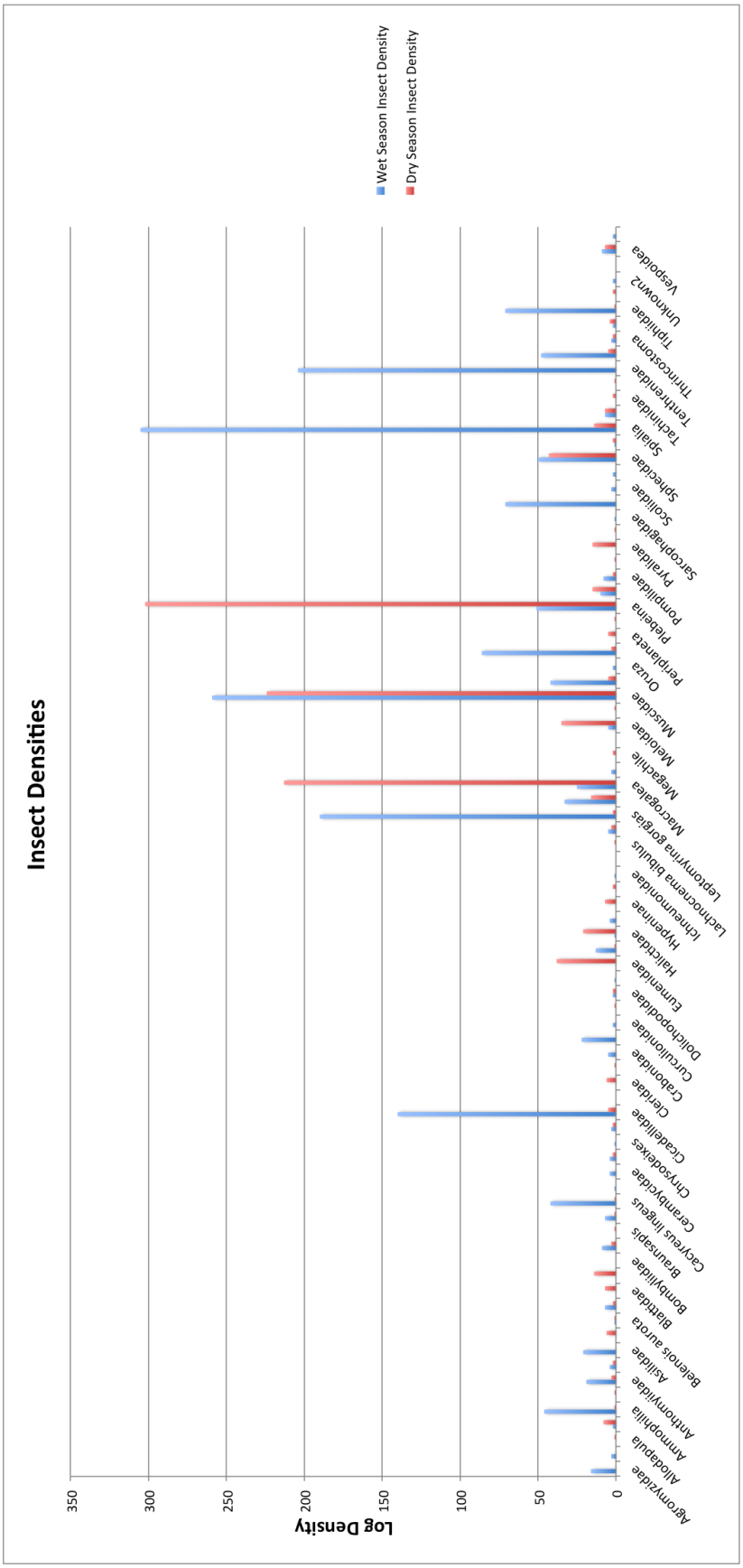
LOCATION	CUPS PLACED		CUPS COLLECTED	
Mesic 1 MEGA	5/4/15	8:15 - 8:45	5/5/15	8:15 - 8:45
Mesic 1 Control	5/4/15	8:45 - 9:15	5/5/15	8:45 - 9:15
Mesic 1 MESO	5/4/15	9:15 - 9:45	5/5/15	9:15 - 9:45
Mesic 1 LMH	5/4/15	9:45 - 10:15	5/5/15	9:45 - 10:15
Intermediate 1 Control	5/6/15	8:30 - 9:00	5/7/15	8:30 - 8:45
Intermediate 1 MESO	5/6/15	9:00 - 9:30	5/7/15	9:00 - 9:30
Intermediate 1 MEGA	5/6/15	9:30 - 10:00	5/7/15	9:30 - 10:00
Intermediate 1 LMH	5/6/15	10:00 - 10:30	5/7/15	10:00 - 10:30
Mesic 2 MEGA	5/9/15	8:15 - 8:45	5/10/15	8:15 - 8:45
Mesic 2 Control	5/9/15	8:45 - 9:15	5/10/15	8:45 - 9:15
Mesic 2 MESO	5/9/15	9:15 - 9:45	5/10/15	9:15 - 9:45
Mesic 2 LMH	5/9/15	9:45 - 10:15	5/10/15	9:45 - 10:15
Arid 1 LMH	5/13/15	9:00 - 9:30	5/14/15	9:00 - 9:30
Arid 1 MEGA	5/13/15	9:30 - 10:00	5/14/15	9:30 - 10:00
Arid 1 MESO	5/13/15	10:00 - 10:30	5/14/15	10:00 - 10:30
Arid 1 Control	5/13/15	10:30 - 11:00	5/14/15	10:30 - 11:00
Intermediate 2 Control	5/15/15	8:30 - 9:00	5/16/15	8:30 - 9:00
Intermediate 2 MEGA	5/15/15	9:00 - 9:30	5/16/15	9:00 - 9:30
Intermediate 2 MESO	5/15/15	9:30 - 10:00	5/16/15	9:30 - 10:00
Intermediate 2 LMH	5/15/15	10:00 - 10:30	5/16/15	10:00 - 10:30
Intermediate 3 LMH	5/20/15	8:30 - 9:00	5/21/15	8:30 - 9:00
Intermediate 3 MEGA	5/20/15	9:00 - 9:30	5/21/15	9:00 - 9:30
Intermediate 3 Control	5/20/15	9:30 - 10:00	5/21/15	9:30 - 10:00
Intermediate 3 MESO	5/20/15	10:00 - 10:30	5/21/15	10:00 - 10:30
Arid 2 MEGA	5/22/15	9:00 - 9:30	5/23/15	9:00 - 9:30
Arid 2 Control	5/22/15	9:30 - 10:00	5/23/15	9:30 - 10:00
Arid 2 MESO	5/22/15	10:00 - 10:30	5/23/15	10:00 - 10:30
Arid 2 LMH	5/22/15	10:30 - 11:00	5/23/15	10:30 - 11:00
Mesic 3 MESO	5/26/15	8:15 - 8:45	5/27/15	8:15 - 8:45
Mesic 3 MEGA	5/26/15	8:45 - 9:15	5/27/15	8:45 - 9:15
Mesic 3 Control	5/26/15	9:15 - 9:45	5/27/15	9:15 - 9:45
Mesic 3 LMH	5/26/15	9:45 - 10:15	5/27/15	9:45 - 10:15
Arid 3 LMH	5/28/15	9:00 - 9:30	5/29/15	9:00 - 9:30
Arid 3 LMH	5/28/15	9:30 - 10:00	5/29/15	9:30 - 10:00
Arid 3 Control	5/28/15	10:00 - 10:30	5/29/15	10:00 - 10:30
Arid 3 MEGA	5/28/15	10:30 - 11:00	5/29/15	10:30 - 11:00

Appendix 3. Total Insect Densities

Insect	Wet Season Density	Dry Season Density	Total Density
Agromyzidae	16	0	16
Agrostis	3	0	3
Allodapula	0	1	1
Amegilla	2	8	10
Ammophilia	46	1	47
Andrenidae	0	1	1
Anthomyiidae	19	3	22
Apis mellifera scutellata	4	2	6
Asilidae	21	0	21
Axiocerces	0	6	6
Belenois aurota	1	1	2
Blaberidae	7	2	9
Blattidae	0	7	7
Blattodea	0	14	14
Bombyliidae	0	0	0
Borbo	9	3	12
Braunsapis	0	1	1
Buprestidae	7	1	8
Cacyreus lingeus	42	1	43
Calliphoridae	1	0	1
Cerambycidae	4	0	4
Chalcididae	4	2	6
Chrysodeixes	1	0	1
Chrysomelidae	3	2	5
Cicadellidae	140	5	145
Cicadidae	0	0	0
Cleridae	0	6	6
Colletes	0	1	1
Crabonidae	5	0	5
Crambidae	22	0	22
Curculionidae	2	0	2
Diptera	0	1	1
Dolichopodidae	2	2	4
Dysdercus	1	0	1
Eumenidae	0	38	38
Evaniidae	13	1	14
Halictidae	1	21	22
Histerdae	4	0	4

Hypeninae	0	7	7
Hypotrigona	0	2	2
Ichneumonidae	1	0	1
Junonia hierta	0	0	0
Lachnocnema bibulus	0	1	1
Lasioglossum	5	3	8
Leptomyrina gorgias	190	2	192
Lipotriches	33	16	49
Macrogalea	25	213	238
Masarinae	3	0	3
Megachile	0	2	2
Megachilidae	0	0	0
Meloidae	5	35	40
Multillidae	0	1	1
Muscidae	259	224	483
Nomia	42	5	47
Oruza	2	0	2
Pentatomidae	86	3	89
Periplaneta	0	5	5
Pinacopteryx eriphia	0	1	1
Plebeina	51	302	353
Polistinae	10	15	25
Pompilidae	8	2	10
Psocoptera	0	1	1
Pyralidae	0	15	15
Reduvidae	0	1	1
Sarcophagidae	1	0	1
Scarabaeidae	71	0	71
Scoliidae	3	0	3
Sesiidae	2	0	2
Sphecidae	50	43	93
Sphex	1	2	3
Spialia	305	14	319
Stratiomyiidae	7	7	14
Tachinidae	0	2	2
Tenebrionidae	0	1	1
Tenthrenidae	204	0	204
Tephritidae	48	5	53
Thrincostoma	3	2	5
Tineidae	2	4	6
Tiphiidae	71	1	72

Unknown1	0	2	2
Unknown2	2	0	2
Vespidae	0	0	0
Vespoidea	9	7	16
Xanthorhoe	2	0	2



Appendix 4. Flower species DCA scores. Loaded DCA scores are in bold.

Flower Species	DCA1	DCA2
Abutilon mauritanium	-1.94178	-0.07767
Acacia brevispica	**3.83392**	**-3.20258**
Acacia brevispica	-0.51344	-0.14776
Acacia drepanolobium	**4.03382**	**-3.5633**
Acacia etibaica	**2.99863**	**-2.59065**
Acacia etibaica	0.59488	1.28146
Acacia mellifera	1.86831	1.84283
Aerva lanata	**4.1127**	**-3.74056**
Aneilema hockii	-0.72429	-0.39074
Asparagus falcatus	-0.65969	-0.90735
Baleria eranthemoides	-1.05861	0.69832
Baleria ramulosa	-0.41855	0.78522
Baleria spinisepla	**3.06947**	**-2.6489**
Becium filamentosum	-1.82297	0.13479
Cleome hirta	-1.57296	0.43498
Commelina erecta	-1.08918	0.02593
Crassula volkensii	**3.09357**	-1.35926
Craterostigma hirsutum	-1.82513	-0.07762
Croton	-1.13841	0.19415
Cyperus	-0.54838	-0.35467
Cyperus	**-2.0233**	0.06016
Emilia discifolia	-0.68371	0.30414
Euphorbia	1.70809	**2.04685**
Euphorbia	**4.46032**	**2.23588**
Evolvolus alsinoides	-0.01086	-0.17294
Evolvolus alsinoides	-0.44284	0.17506
Gloriosa superba	-1.68035	-0.34559
Grewia similis	-0.01086	-0.17294
Gutenbergia cordifolia	**-2.0417**	0.09272
Helichyrusum glumaceum	1.49786	-1.89785
Hibiscus callyphulus	1.45227	-1.87515
Hibiscus flavifolius	-1.13488	-0.53546
Indigofera	-0.8432	-0.32987
Indigofera	0.18536	-0.16401
Ipomoea kituensis	**3.49718**	1.95244
Ipomoea sinensis	1.49802	-0.8975
Ipomoea sinensis	**-2.94041**	-0.03062
Justicia odora	**3.97011**	**-3.79966**
Justicia odora	0.35271	-1.14073

Kalanchoe lanceolata	**2.36352**	**-2.38314**
Kalanchoe pritwizii	**3.37521**	**-2.09451**
Kleinia squarossa	**4.1127**	**-3.74056**
Kleinia squarossa	**2.95363**	-0.18039
Kleinia squarossa	-0.21971	0.95276
Lily	**-2.07892**	-0.1092
Lippia javanica	-1.04143	0.20508
Maerua angolensis	**4.39748**	1.65464
Notonia petraea	**2.1702**	1.81552
Opuntia stricta	-1.40311	-0.44796
Ornithogalum tenuifolium	1.59302	1.81059
Osteospermum vaillantii	**-2.69647**	0.07082
Oxygonum sinuatum	**-2.01264**	-0.00473
Pavonia patens	-0.70936	-0.16426
Pavonia patens	-0.05748	0.85945
Pentanisia ouranogye	**-2.61941**	-0.03643
Perlagonium whytei	-0.56613	0.87893
Phyllanthus maderaspatensis	**4.1127**	**-3.74056**
Phyllostria	**-2.33691**	0.29159
Plectranthus caninus	1.51007	-1.95358
Plectranthus comosus	0.66125	-0.74107
Plectranthus cylindraceus	**2.62944**	-0.4935
Plectranthus montanus	1.13132	-0.92194
Plectranthus prostatus	**4.03492**	**-3.7728**
Plicosephalus saggitifolius	1.83274	1.65322
Polygala sphenoptera	-1.34439	0.05346
Polygala sphenoptera	0.53102	1.50709
Portulaca foliosa	1.23678	-1.46463
Priva curtisii	-1.36851	0.17016
Sarcostemma viminale	**3.71402**	**-2.01537**
Solanum	-0.10406	0.26076
Trubulus terrestis	**-2.71125**	-0.03599
Unknown 1	-1.70316	0.06432

Appendix 5. Insect species DCA scores. Loaded DCA scores are in bold.

Insect ID	DCA1	DCA2
Agromyzidae	-0.31911	1.72823
Agrostis	-1.55041	0.31887
Allodapula	1.02902	-0.74316
Amegilla	0.75224	0.42257
Ammophilia	0.1498	1.77657
Andrenidae	1.94363	-0.40794
Anthomyiidae	-0.43638	1.69115
Apis mellifera scutellata	-0.01384	1.06071
Asilidae	-0.55446	1.50656
Axiocerces	1.9893	0.21076
Belenois aurota	1.31096	1.07783
Blaberidae	-0.05133	-1.34955
Blattidae	**2.2259**	-0.15402
Blattodea	**2.09068**	-0.28195
Borbo	0.03051	-1.66074
Braunsapis	**2.40797**	-0.51162
Buprestidae	0.00448	1.21581
Cacyreus lingeus	-0.68002	**2.43068**
Calliphoridae	-1.97881	-0.71107
Cerambycidae	**-2.06867**	-0.12606
Chalcididae	-0.05384	0.2853
Chrysodeixes	**-2.27507**	-0.71192
Chrysomelidae	0.28359	1.66279
Cicadellidae	-1.6776	0.54039
Cleridae	1.8616	-0.52848
Colletes	**2.59272**	0.28422
Crabonidae	-0.72784	-1.93134
Crambidae	-0.96288	**2.07133**
Curculionidae	-1.29467	**2.18933**
Diptera	1.94363	-0.40794
Dolichopodidae	-0.31988	-1.55477
Dysdercus	-1.21693	-1.38028
Eumenidae	**2.17902**	0.60053
Evaniidae	-0.32037	1.66956
Halictidae	1.69127	-0.08209
Histerdae	-0.10153	-1.45671
Hypeninae	**2.66122**	0.11705
Hypotrigona	1.02902	-0.74316
Ichneumonidae	-1.25984	1.19917
Lachnocnema bibulus	1.86819	0.90611

Lasioglossum	-0.55819	-1.17143
Leptomyrina gorgias	-1.79498	0.33641
Lipotriches	-0.54732	-0.40935
Macrogalea	1.79999	0.23506
Masarinae	-0.21609	**-2.08583**
Megachile	**2.01019**	0.18255
Meloidae	**2.02286**	-0.3325
Multillidae	**2.28373**	-0.20764
Muscidae	0.48856	0.19046
Nomia	-1.2129	-0.57302
Oruza	**-2.51297**	-0.45575
Pentatomidae	-1.04073	0.1305
Periplaneta	**2.19787**	-0.18204
Pinacopteryx eriphia	1.86819	0.90611
Plebeina	**2.06658**	-0.23666
Polistinae	0.78158	1.77906
Pompilidae	-0.53224	0.21702
Psocoptera	1.02902	-0.74316
Pyralidae	**2.35537**	0.03448
Reduvidae	**2.40797**	-0.51162
Sarcophagidae	-0.76099	**-2.28287**
Scarabaeidae	**-2.53284**	0.22144
Scoliidae	-0.43041	**-2.15151**
Sesiidae	-0.4752	-1.88897
Sphecidae	0.75431	-1.34503
Sphex	0.41297	0.31632
Spialia	-1.44028	-0.73784
Stratiomyiidae	0.1268	1.68306
Tachinidae	1.90091	0.49825
Tenebrionidae	1.75906	0.26544
Tenthrenidae	-0.4268	-1.96619
Tephritidae	-0.99493	0.5281
Thrincostoma	-0.89316	0.38194
Tineidae	1.11493	0.2141
Tiphiidae	-0.30311	1.8865
Unknown1	**2.6031**	-0.37138
Unknown2	-0.75207	-1.71506
Vespoidea	0.6474	**2.03938**
Xanthorhoe	-1.00356	-1.69893